

## Amplitude-Dependent Frequency, Desynchronization, and Stabilization in Noisy Metapopulation Dynamics

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The enigmatic stability of population oscillations within ecological systems is analyzed. The underlying mechanism is presented in the framework of two interacting species free to migrate between two spatial patches. It is shown that the combined effects of migration and noise cannot account for the stabilization. The missing ingredient is the dependence of the oscillations' frequency upon their amplitude. A simple model of diffusively coupled oscillators allows the derivation of quantitative results, like the functional dependence of the desynchronization upon diffusion strength and frequency differences. The oscillations' amplitude is shown to be (almost) noise independent.

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The apparent stability of prey-predator systems is an age-old puzzle. When a predator consumes a prey it clearly increases its fitness and its chance to breed and to produce more predators, so one may expect that system to be inherently unstable. Ancient day naturalists, like Herodotus and Cicero, perceived the persistence of prey species in the face of adversity as a manifestation of divine power and the creator's design [1]. In modern times, the explanations become more deterministic, and rely on the fact that when the prey population decays there is not enough food for the predators and their population also diminishes. This idea naturally leads to the concept of population oscillations and was expressed mathematically, using deterministic continuous time partial differential equations, by Lotka and Volterra (LV) model [2]. The analogous model with discrete time step was introduced for a parasitoid-host system by Nicholson and Bailey [3]. Both models allow, essentially, for population oscillations around a coexistence steady state.

Lotka, Volterra, and Nicholson recognized that the oscillations described by their models are not stable [1,4]. The Nicholson-Bailey map admits an unstable steady state; for the LV system, the fixed point is marginally stable, rendering the system extinction-prone for any noise amplitude. Indeed, experimental and theoretical studies of both systems reveal that the oscillations increase in size until one of the species becomes extinct [5,6]. Spatially extended systems, on the other hand, seem to support sustained oscillations, as emphasized by field studies [7], experiments, [8], and numerics [9].

These findings give an appeal to Nicholson's [4] old proposal about migration-induced stabilization, i.e., that desynchronization between weakly coupled spatial patches, together with the effect of migration, stabilize the global populations. Unfortunately, examination of this idea in many studies, summarized in a recent review article [10], yields negative results. Generically, diffusion stabilizes the homogenous manifold and different spatial patches

get synchronized, leading back to the well-mixed unstable dynamics [11]. Diffusion induced instability may occur if the migration rate of the predator is much smaller than that of the prey [12], or in a case where the reaction parameters vary on different spatial patches [13]. Neither of these conditions explains the results in homogenous systems considered in [8,9]. It seems that the *combined* effect of noise and diffusion is a necessary precondition for population stabilization. However, up until now the qualitative nature of the underlying mechanism has remained obscure, and no theoretical framework that allows for quantitative prediction has been presented.

Let us demonstrate the stability problem using the paradigmatic LV model [2]. The model describes the time evolution of two interacting populations: a prey ( $b$ ) population that grows with a constant birth rate  $\sigma$  in the absence of a predator, and a predator population ( $a$ ) that decays (with death rate  $\mu$ ) in the absence of a prey. Upon encounter, the predator may consume the prey with a certain probability. For a well-mixed population, the corresponding PDE's are

$$\frac{\partial a}{\partial t} = -\mu a + \lambda_1 ab, \quad \frac{\partial b}{\partial t} = \sigma b - \lambda_2 ab, \quad (1)$$

where  $\lambda_1$  and  $\lambda_2$  are the relative increase (decrease) of the predator (prey) populations due to the interaction between species, correspondingly.

The system admits two unstable fixed points: the absorbing state  $a = b = 0$  and the state  $a = 0, b = \infty$ . There is one marginally stable fixed point at  $\bar{a} = \sigma/\lambda_2, \bar{b} = \mu/\lambda_1$ . The system supports a conserved quantity  $H$ ,

$$H = \lambda_1 b + \lambda_2 a - \mu \ln(a) - \sigma \ln(b), \quad (2)$$

and the phase space is segregated into a collection of nested one-dimensional trajectories as illustrated in Fig. 1. Without loss of generality, we employ hereon the symmetric parameters  $\mu = \sigma = \lambda_1 = \lambda_2 = 1$ .

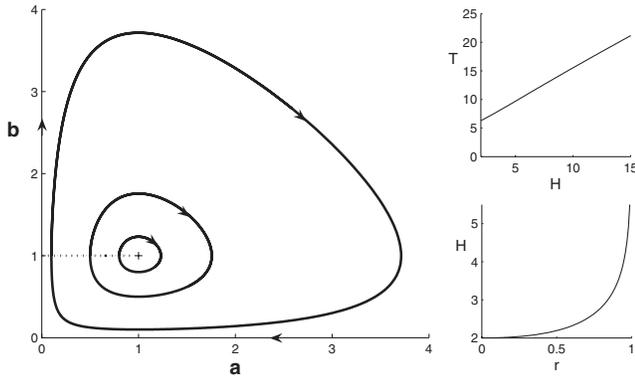


FIG. 1. The LV phase space (left panel) admits a marginally stable fixed point surrounded by close trajectories (three of these are plotted). Each trajectory corresponds to single  $H$  defined in Eq. (2), where  $H$  increases monotonically along the (dashed) line connecting the center with the  $a = 0$  wall, as shown in the lower right panel. In the upper right panel, the period of a cycle  $T$  is plotted against  $H$ , and is shown to increase almost linearly.

Given the integrability of that system, the effect of noise is quite trivial; the system wanders between trajectories, thus performing random walk in  $H$ . The amplitude of oscillation is growing, and extinction occurs when the trajectory hits the zero population state for one of the species. In Fig. 2, the survival probability  $Q(t)$  (the probability that a trajectory does not hit the absorbing walls until  $t$ ) is shown for different noise amplitudes.

Our first observation is that these stability features change dramatically if the system is *not* well mixed. The simplest example is the LV system on two patches ( $i, j \in \{1, 2\}$ ):

$$\begin{aligned} \frac{\partial a_i}{\partial t} &= -\mu a_i + \lambda_i a_i b_i + D_a(a_j - a_i) \\ \frac{\partial b_i}{\partial t} &= \sigma b_i - \lambda_i a_i b_i + D_b(b_j - b_i). \end{aligned} \quad (3)$$

The invariant manifold is the two dimensional subspace  $a_1 = a_2, b_1 = b_2$ . The time evolution of that system, with an additive noise [14], equal diffusivities and symmetric reaction rates is obtained through Euler integration. In the limit  $D = 0$  the patches decouple while if  $D = \infty$  they act like a single patch, and in both situations the system goes extinct. However, between these two extremes, there is a region where the *combined* effect of diffusion and noise stabilizes a finite region within the invariant manifold, as demonstrated in Fig. 3.

The LV system is somewhat complicated, since the angular velocity depends not only on  $H$ , but also on the location along a trajectory. In order to clarify the origin of the stable cycles, let us introduce a toy model that imitates the main features of the real systems. Although that model does not allow for an absorbing state, it captures the basic mechanism for stabilization of spatially extended systems in the presence of noise.

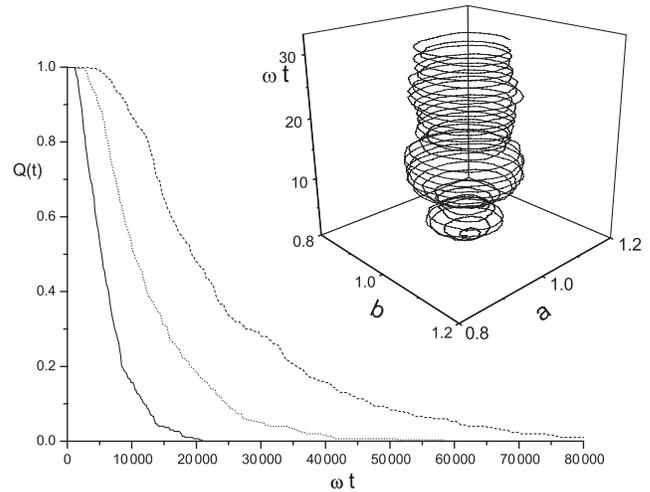


FIG. 2. The survival probability  $Q(t)$  is plotted versus time for a single patch noisy LV system. Equations (1) (with the symmetric parameters) were integrated numerically (Euler integration with time step 0.001), where the initial conditions are at the fixed point  $a = b = 1$ . At each time step, a small random number  $\eta(t)\Delta t$  was added to each population density, where  $\eta(t) \in [-\Delta, \Delta]$ . A typical phase space trajectory, for  $\Delta = 0.5$ , is shown in the inset. Using 300 different noise histories, the survival probability is shown here for  $\Delta = 0.5$  (full line),  $\Delta = 0.3$  (dotted line) and  $\Delta = 0.25$  (dashed line). Clearly,  $Q(t)$  decays exponentially at long times,  $Q(t) \sim \exp(-t/\tau)$ , where  $1/\tau$  scales with  $\Delta^2$ .

The toy model deals with the phase space behavior of diffusively coupled oscillators, where the angular frequency depends on the radius of oscillations. With additive noise, the Langevin equations take the form,

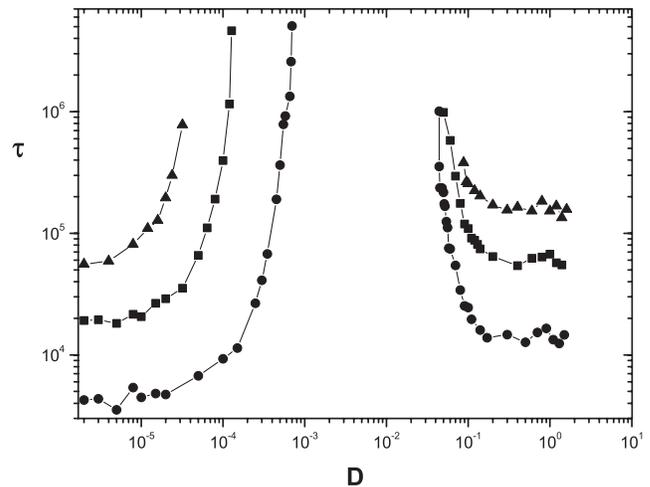


FIG. 3. The typical persistence time as a function of the diffusion rate for different levels of noise. The values of  $\tau$  were gathered from survival probability plots (like those in Fig. 1) and are displayed here for the two-patch system.  $\tau$  grows very rapidly with the migration rate for small diffusion values, and decays with  $D$  for large diffusivities. Data is shown for different noise intensities  $\Delta = 0.3$  (triangles),  $0.5$  (squares), and  $1.0$  (circles).

$$\begin{aligned}\frac{\partial x_i}{\partial t} &= \omega(x_i, y_i)y_i + D_1(x_j - x_i) + \eta_{x,i}(t), \\ \frac{\partial y_i}{\partial t} &= -\omega(x_i, y_i)x_i + D_2(y_j - y_i) + \eta_{y,i}(t),\end{aligned}\quad (4)$$

where all the  $\eta$ 's are taken from the same distribution. If the angular frequency is location independent,  $\omega(x, y) = \omega_0$ , the problem is reduced to coupled *harmonic* oscillators, a diagonalizable linear problem that admits two purely imaginary eigenvalues in the invariant, homogenous manifold. With noise, the random walk on that manifold is independent of the motion in the fast manifold and the oscillation radius diverges with the square root of time.

Now let us define the oscillation radius for each patch,  $r_i = \sqrt{x_i^2 + y_i^2}$  for  $i = 1, 2$ , and assume that the angular frequency depends only on that radius and is  $\theta$  independent [ $\theta_i \equiv \arctan(y_i/x_i)$ ]. With that, the total phase  $\Phi = \theta_1 + \theta_2$  decouples and the three-dimensional phase space motion is dictated by the equations (we take  $D_1 = D_2 = D$  and define  $\phi = \theta_1 - \theta_2$ ,  $R \equiv r_1 + r_2$ ,  $r \equiv r_1 - r_2$ ):

$$\dot{R} = -2D\sin^2(\phi/2)R + \tilde{\eta}_R, \quad (5)$$

$$\dot{r} = -2D\cos^2(\phi/2)r + \tilde{\eta}_r, \quad (6)$$

$$\dot{\phi} = -2D\left(\frac{R^2 + r^2}{R^2 - r^2}\right)\sin\phi + \omega(r_2) - \omega(r_1) + \left(\frac{\tilde{\eta}_1}{r_1} - \frac{\tilde{\eta}_2}{r_2}\right). \quad (7)$$

As before, all the  $\tilde{\eta}$ 's are taken from the same distribution.

Equations (5)–(7) clarify the role of desynchronization as the stabilizing mechanism. The dynamics in the homogenous ( $R$ ) manifold look very much like that of an overdamped harmonic oscillator in noisy environment,  $\dot{z} = -kz + \eta(t)$ , that admits the steady state Boltzman distribution  $P(z) \sim \exp(-kz^2/\Delta^2)$ . However, if the phases of these two patches synchronize and the expectation value of  $\phi^2$  vanishes, so does the “spring constant” of the oscillator. Without that restoring force, the motion on the  $R$  manifold is a simple random walk, so the oscillation amplitude grows indefinitely. Phase ( $\phi$ ) desynchronization, thus, is the crucial condition for stabilization. This feature is stressed in the inset of Fig. 4, where the flow lines of the deterministic dynamics in the  $R - \phi$  plane are sketched: the line  $\phi = 0$  is marginally stable, but any deviation leads to inward flow.

Close to the invariant manifold, when  $\phi$  and  $r/R$  are much smaller than 1, the amplitude desynchronization  $r$  is solvable. Neglecting corrections of order  $\phi^2$ ,  $\dot{r} = -2Dr + \eta$ , which is again an equation for an overdamped harmonic oscillator, so  $P(r) \sim \exp(-Dr^2/\Delta^2)$  and the  $r^2$  typical fluctuation around zero is of order  $\Delta^2/D$ . However, the amplitude desynchronization factor  $r$  does not appear in (5), and the stabilization is determined only by the phase. Accordingly, the system supports an attractive manifold iff the amplitude desynchronization yields phase desynchronization.

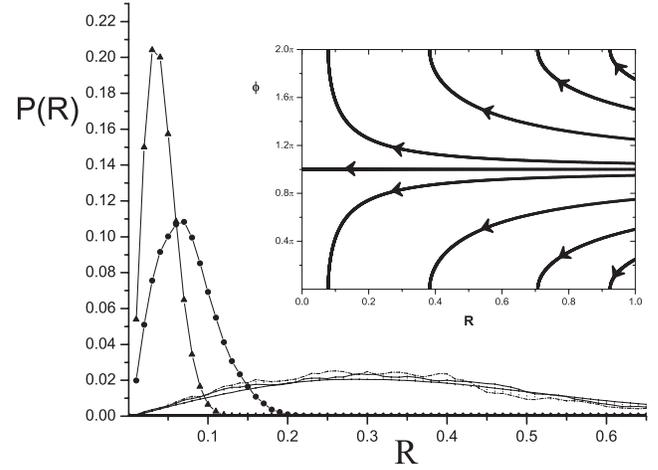


FIG. 4. Histograms showing the probability to be at a distance  $R$  from the origin as a function of  $R$ , for two coupled noisy oscillators, where  $\omega = 1 + ar$  with  $D = 0.01$ , and various values of noise strength  $\Delta$ , and angular velocity gradient  $\alpha$ . As expected, the phase space confinement is proportional to  $\alpha$ , from  $\alpha = 1$  (triangles) to  $\alpha = 0.5$  (circles) to  $\alpha = 0.1$  (solid line), all for the same level of noise  $\Delta = 0.1$ . On the other hand, as predicted by the linear analysis close to the invariant manifold, the confinement is noise independent, and the three solid lines corresponding to different levels of noise ( $\Delta = 0.1, 0.5, 1$  with the same  $\alpha = 0.1$ ) almost coincide. The inset shows the flow lines on the  $r = 0$  plane. The invariant manifold  $\phi = 0$  is marginally stable, but there is some flow towards the center for any finite  $\phi$ .

Another piece of information may be gathered from the harmonic limit,  $\omega(r) = \omega_0$ . Here there should be no phase synchronization, as we already diagonalized the linear equation and find no restoring term in the homogenous plane. Looking at Eq. (7) with  $\omega(r_1) - \omega(r_2) = 0$ , one concludes that the rightmost (noise) term in (7) is irrelevant. The dependence of the frequency on the amplitude (i.e., the dependence of  $\omega$  on  $r$ ) should be the factor that allows the translation of amplitude desynchronization into a phase desynchronization. Intuitively, when two patches with different oscillation amplitudes move with different angular velocities, this immediately yields phase differences.

Without the noise term, Eq. (7) may be written as,

$$\dot{\phi} = -2D\left(\frac{R^2 + r^2}{R^2 - r^2}\right)\sin\phi - r\frac{\partial\omega}{\partial r} \approx -2D\phi - r\frac{\partial\omega}{\partial r}, \quad (8)$$

where the approximation is valid close to the invariant manifold. Again, we face an overdamped harmonic oscillator, where now the source of noise is the  $r$  fluctuations (obeying the Boltzman statistics). With that,  $\langle\phi^2\rangle \sim [\omega'(r)]^2\Delta^2/D^3$  may be plugged into (5)

$$\dot{R} = -2D\sin^2(\phi/2)R + \tilde{\eta}_R \approx -D\langle\phi^2\rangle R/2 + \tilde{\eta}_R, \quad (9)$$

and one finds  $\langle R^2 \rangle \sim [D/\omega'(r)]^2$ . This radius of stable oscillations diverges as  $D \rightarrow \infty$ , as expected. The small

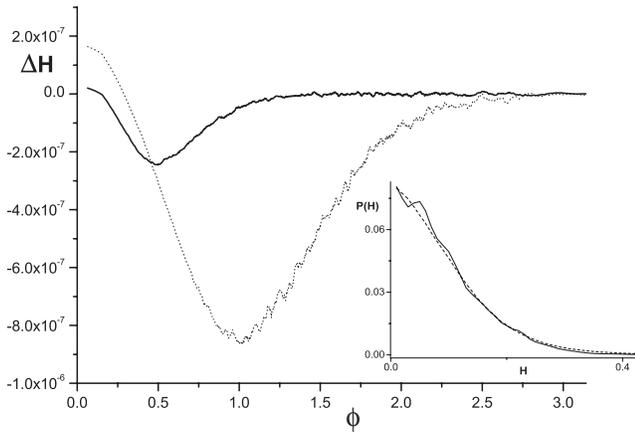


FIG. 5. The average  $\Delta H$  at an elementary time step (0.001 of a unit time) as a function of the angle  $\phi$  between the patches. While a simple phase space random walk yields on average positive  $\Delta H$ , this property is shown here to hold only for small  $\phi$ . At larger angles, the diffusion between patches forces the system toward the center and the average  $\Delta H$  becomes negative. Results are shown for  $\Delta = 0.1$  (full line) and  $\Delta = 1$  (dashed line). The inset shows the probability distribution function for  $H$  at these two noise levels.

$D$  instability (decoupled patches) manifests itself in the divergence of  $\langle r^2 \rangle$  as  $D \rightarrow 0$ . Surprisingly, since both the restoring force and the noise in the invariant manifold are proportional to  $\Delta^2$ , the expected  $R$  distribution has to be *noise independent* at that limit, as demonstrated in Figs. 4 and 5.

Equations (4) may be generalized to include the case of an unstable focus. The same analysis [15] shows that, for small noise and small repulsion, a noise-induced transition will occur at  $\epsilon \sim (\omega^2 \Delta^2 / D^2)$ , where  $\epsilon$  is the Liapunov exponent. If the noise is small enough, the desynchronization is weak and the system is rendered extinction prone. Strong noise, conversely, stabilizes the system and ensures conservation. The mechanism presented here is thus relevant to any system where the local dynamic admits an unstable focus (e.g., above Hopf bifurcation), provided that the spatial coupling is *diffusive*.

Now let us check our predictions for the LV system. At the vicinity of the homogenous fixed point, the dynamic is similar to a single patch dynamic. The square of the average distance from the fixed point grows linearly with time at the beginning, with a slope that depends on the noise amplitude, as expected for the random walk in the invariant manifold scenario. For “intermediate” migration (e.g.,  $D = 0.01$ ), the average distance from the origin saturates, while the chance to find the system at large  $H$  becomes exponentially small, as illustrated in Fig. 5. In agreement with the results of the toy model, the flow toward the center is correlated with the phase desynchronization, leading to stabilization at finite  $H$ . As predicted, while the width of the  $\phi^2$  distribution depends strongly on

the noise amplitude, the oscillation amplitude is almost noise independent.

In conclusion, we suggest a novel solution to a long-standing conundrum: the stabilization of a noisy unstable dynamical system on spatial domains. The basic feature that leads to stabilization is the dependence of angular velocity on phase space coordinates. This dependence allows the noise to desynchronize spatially coupled patches, and then migration decreases concentration gradients and causes an inward flow.

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